

Influence of Vegetation Type on the Constitution of Terrestrial Gastropod Communities in Northwest Spain

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Abstract. We investigated the influence of three different vegetation types on the establishment of terrestrial gastropod communities in the northwest Iberian Peninsula, using both an ordination technique (Detrended Correspondence Analysis) and a classification technique (Two-Way Indicator Species Analysis) applied to a 498×47 site-by-species abundance matrix (total number of individuals 17,902). The results of these analyses indicate that meadow sites are characterized by a group of species comprising *Cionella lubrica* (Müller, 1774), *Nesovitrea hammonis* (Ström, 1765), and *Zonitoides excavatus* (Alder, 1830). Woodland sites are characterized by a group comprising *Columella aspera* Waldén, 1966, *Oxychilus alliarius* (Miller, 1822), *Acanthinula aculeata* (Müller, 1774), and *Punctum pygmaeum* (Draparnaud, 1801). *Vitrea contracta* (Westerlund, 1871), *Discus rotundatus*, and *Aegopinella nitidula* (Draparnaud, 1805) form a group of companion species to this latter community.

INTRODUCTION

The view that vegetation type affects the distribution of terrestrial gastropods has been advanced from various angles and conclusions by authors including Bába, 1974; Beyer & Saari, 1977; André, 1982; Štamol, 1991, 1993; Cowie et al., 1995, and Hermida et al., 1995. Some authors have suggested that distribution is not primarily related to vegetation but rather to litter characteristics (Bishop, 1977; Locasciulli & Boag, 1987). By contrast, other authors have gone so far as to define gastropod communities corresponding to specified phytosociological communities (Frank, 1981; Kornig, 1989; Štamol, 1992; Bába & Bagi, 1997). It has also been suggested that microhabitat characteristics are the most important determinants of gastropod distribution (Drozdowski, 1968; Boag & Wishart, 1982; Young & Evans, 1991).

Most studies in this field are based on simple descriptions of the habitats in which different gastropod species are found, and relatively few studies have applied quantitative methods. In the present study, with the aim of furthering understanding of the influence of vegetation type on the distribution of terrestrial gastropods, we collected 498 samples from three biotopes (woodland, meadow, riverbank) in the northwest Iberian Peninsula (Figure 1). These three biotopes have distinct characteristics, and could be expected to have distinct malacofaunas. The data were analyzed with the aid of an ordination technique

(Detrended Correspondence Analysis) and a hierarchical classification technique (TWINSPAN).

DESCRIPTION OF THE STUDY AREA

The study area (12,400 km²) comprises the Provinces of A Coruña and Pontevedra in western Galicia (northwest Spain) (Figure 1). This area is bounded to the east by a mountain system running north-south and reaching elevations of up to 1100 m. Soils are generally poor, in view of the predominance of granites and schists, together with the high rainfall and hilly topography: cambisols, leptosols, and regosols are the most frequent. Climate is oceanic, characterized by high rainfall and mild temperatures. The potential vegetation over most of the study area (which falls within the Eurosiberian Region) is *Quercus robur* L. woodland. Depending on series, the codominant tree species may be *Betula pubescens* Ehrh. or *Castanea sativa* Miller, with *Laurus nobilis* L., *Ilex aquifolium* L., *Crataegus monogyna* Jacq., or *Frangus alnus* Miller in the shrub layer. However, much of the study region is currently occupied by the introduced species *Pinus pinaster* Aiton, *P. radiata* D., and *Eucalyptus globulus* Labill.

Riverbank vegetation is strongly influenced by groundwater level, with two different associations being recognized, both dominated by *Alnus glutinosa* (L.), namely *Valeriano pyrenaicae-Alnetum glutinosae*, richer in ferns

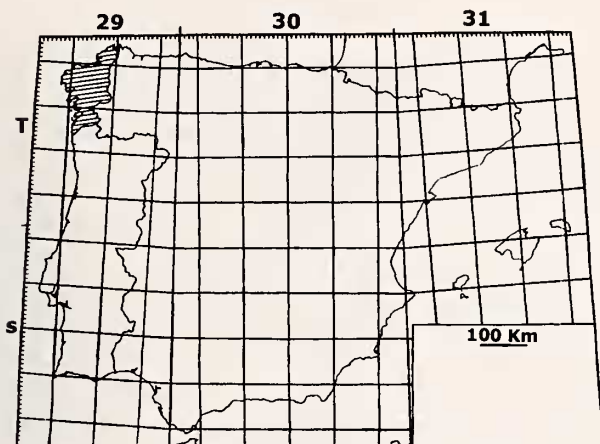


Figure 1

Location of the study area showing the 100 km squares of the UTM (Universal Transversal Mercator) Grid.

and nemoral herbs, and the more disturbed *Senecio bay-onesis-Alnetum glutinosae*.

Meadow vegetation in the study area falls into the phytosociological class *Molinio-Arrhenatheretea elatioris*. The most frequent species within this association include *Agrostis capillaris* L., *Linum bienne* Miller, *Lolium perenne* L., *Trifolium dubium* Sibth., *Bellis perennis* L., *Plantago lanceolata* L., and *Holcus lanatus* L.

MATERIALS AND METHODS

Samples were collected, by stratified random sampling, from a total of 498 woodland, riverbank, and meadow sites (166 sites in each biotope). At each site we obtained a soil and litter sample of 100 × 50 × 5 cm (length × width × depth). In the laboratory, the samples were wet-sieved through a 7 mm mesh over a 0.5 mm mesh. Material retained by the second sieve was carefully examined under a magnifying glass, with the aim of finding all gastropods. Gastropods found were immersed in water, then fixed in 70° alcohol. Only live specimens were included, since otherwise the abundance of testaceous species is likely to be overestimated (André, 1981; Phillipson & Abel, 1983). The 47 species found, together with the species codes used in the tables and figures, are listed in Appendix I.

The resulting 498 × 47 site-by-species abundance matrix was analyzed by Detrended Correspondence Analysis. DCA is a modification of Correspondence Analysis (CA) developed to overcome some conspicuous faults. The main modification, from which the technique obtains its name, is detrending, which attempts to remove the "arch effect" in which the second and subsequent axes appear as polynomial functions of the first axis and thus obscure the underlying gradient structure (Ter Braak, 1986, 1988).

The analysis was performed with CANOCO 3.1 (Ter Braak, 1990) using the rare-species downweighting option, by which all species with frequency below 20% of the maximum frequency of any species are downweighted in proportion to their frequency (Hill, 1979). For this analysis, the data matrix was first log-transformed ($\log[n + 1]$, where n is number of individuals).

CANOCO can supply centroids (weighted averages) of environmental variables in the ordination diagram. To find out the centroids, a matrix was built in which the variable biotope was converted into a nominal variable, so that it was possible to represent it by points in the ordination diagram (Ter Braak, 1988).

To verify the results obtained by ordination, we used a divisive hierarchical classification technique (Two-Way Indicator Species Analysis, TWINSpan; Hill, 1979).

One of the basic ideas in TWINSpan stems is that each group of sites can be characterized by a group of differential species, species that appear to prevail in one side of a dichotomy. The idea of a differential species is essentially qualitative, and to be effective with quantitative data must be replaced by a quantitative equivalent. This equivalent is the "pseudospecies." Each species abundance is replaced by the presence of one or more pseudospecies. The more abundant a species is, the more pseudospecies are defined. The levels of abundance that are used in TWINSpan to define the crude scale are here termed "pseudospecies cut levels."

RESULTS

Ordination

The results of correspondence analysis of the log-transformed 498 × 47 site-by-species matrix are summarized in Figure 2 and Tables 1 and 2. The first four axes explained the majority of total variance. Significance was calculated using a χ^2 procedure.

Absolute contribution values for each species were calculated according to Judez (1989). Assuming that the 47 taxa have the same absolute contribution (defined as uniform absolute contribution), every species would contribute with 2.12% to the total variance of a single axis (100/47). Species with absolute contribution value higher than 2.12% would be the ones which better explain the axes (Judez, 1989). Such species are listed for axes I and II in Table 3.

The interpretation of the results of this analysis in terms of potential cause-effect hypotheses is made difficult by the large number of samples and species, and by the low inertias of the first three axes (despite their statistical significance). With the aim of reducing data noise and better revealing the data structure, we thus performed a second analysis (Figure 3) using those species that were not downweighted, i.e., species that had been assigned a downweighting factor of 1, namely, *Acanthinula aculeata*, *Arion intermedius*, *Aegopinella nitidula*, *Coumella as-*

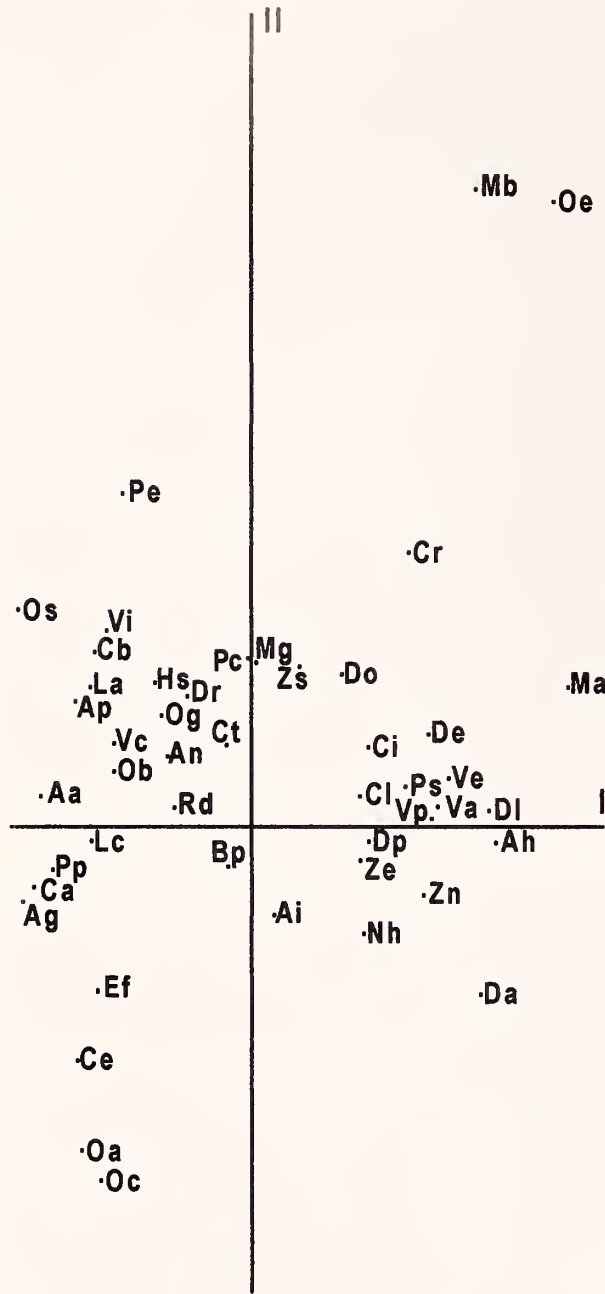


Figure 2

Ordination of the 47 species on the first two axes extracted by Detrended Correspondence Analysis.

pera, *Cionella lubrica*, *Carychium tridentatum*, *Discus rotundatus*, *Nesovitrea hammonis*, *Oxychilus alliarjrus*, *Punctum pygmaeum*, *Vitrea contracta* and *Zonitoides excavatus* (Table 1). Eigenvalues (measure of separation of the species distributions along the ordination axis), percentage inertias, χ^2 values, and degrees of freedom are listed in Table 4.

Table 1

Downweighting values for each of the 47 species, as calculated by CANOCO.

| | | | | | | | |
|----|------|----|-------|----|-------|----|-------|
| Aa | 1.00 | De | 0.966 | Os | 0.355 | Ma | 0.095 |
| Ai | 1.00 | Do | 0.836 | Pu | 0.281 | Eb | 0.059 |
| An | 1.00 | Ef | 0.787 | Zs | 0.268 | Ap | 0.053 |
| Ca | 1.00 | Ob | 0.775 | Ci | 0.265 | Ag | 0.029 |
| Ci | 1.00 | Ps | 0.751 | Oc | 0.237 | Ce | 0.029 |
| Ct | 1.00 | DI | 0.659 | Ve | 0.234 | Da | 0.029 |
| Dr | 1.00 | Cb | 0.656 | Mg | 0.203 | Dp | 0.029 |
| Nh | 1.00 | Lc | 0.650 | Og | 0.174 | Pe | 0.029 |
| Oa | 1.00 | Hs | 0.459 | Vi | 0.161 | Rd | 0.029 |
| Pp | 1.00 | Vp | 0.477 | Ah | 0.128 | Va | 0.029 |
| Vc | 1.00 | Cr | 0.468 | Bp | 0.112 | Zn | 0.029 |
| Ze | 1.00 | Oe | 0.394 | La | 0.096 | | |

The absolute contribution values for each species on axes I and II were calculated (Judez, 1989) and listed in Table 5. Species with absolute contribution value higher than 8.3% (100/12) are indicated in bold. For axis I, these species are (in decreasing order of contribution) *N. hammonis*, *C. lubrica*, *C. aspera*, *A. aculeata*, *Z. excavatus*, and *O. alliarjrus*, which together explain 77% of the variance on this axis. For axis II, these species are *A. intermedius*, *O. alliarjrus*, *D. rotundatus*, and *C. tridentatum*, which together explain 84% of variance on this axis. We base our interpretation on axis I, since axis II was not significant at the 5% level (Judez, 1989).

According to Figure 3, it can be seen that there is a group of three species (*N. hammonis*, *Z. excavatus*, and *C. lubrica*) which can be clearly differentiated from the rest in relation to their position along the axis. Toward the far right side of this axis, *C. aspera*, *P. pygmaeum*, and *A. aculeata* show a high correlation with this axis, although *A. nitidula* and *V. contracta* also show certain proximity, but with lower contributions to axis I. The two species with lowest absolute contributions to axis I were *C. tridentatum* and *A. intermedius*, which located close to the origin of this axis. *O. alliarjrus* shows a higher contribution to axis II than to axis I.

In the plot of sites (Figure 4), most of the woodland sites are located on the right side of axis I, whereas most

Table 2

Eigenvalues, percentage inertias, significance levels, and degrees of freedom for the first four axes extracted by DCA of the 498 × 47 site-by-species abundance matrix.

| Axis | Eigenvalue | % Inertia | χ^2 | df |
|------|------------|-----------|----------|-----|
| I | 0.4018 | 8.4 | < 0.01 | 491 |
| II | 0.2802 | 5.8 | < 0.01 | 489 |
| III | 0.2663 | 5.6 | < 0.05 | 487 |
| IV | 0.2323 | 4.8 | > 0.05 | 485 |

Table 3

Coordinates, weights, and absolute contributions to the first two axes extracted by DCA of the 498×47 matrix (see Table 2), for the 18 species whose contribution to at least one of these axes was greater than the average.

| Species | Coord. axis I | Coord. axis II | Weight | Contrib. axis I (%) | Contrib. axis II (%) |
|------------------------|---------------|----------------|--------|---------------------|----------------------|
| <i>A. aculeata</i> | -1.7307 | 0.2755 | 0.0270 | 8.0873 | 0.2049 |
| <i>A. intermedius</i> | 0.1809 | -0.7525 | 0.1129 | 0.3694 | 6.3930 |
| <i>A. nitidula</i> | -0.6896 | 0.6063 | 0.0909 | 4.3227 | 3.3414 |
| <i>C. aspera</i> | -1.8361 | -0.5628 | 0.0280 | 9.4395 | 0.8868 |
| <i>C. lubrica</i> | 0.9731 | 0.2486 | 0.1255 | 11.8838 | 0.7756 |
| <i>C. barbara</i> | 1.3789 | 2.3641 | 0.0068 | 1.2929 | 3.8004 |
| <i>C. tridentatum</i> | -0.2055 | 0.7473 | 0.1030 | 0.4349 | 5.7521 |
| <i>D. reticulatum</i> | 1.5687 | 0.7886 | 0.0150 | 3.6912 | 0.9328 |
| <i>D. lombricoides</i> | 2.0974 | 0.1239 | 0.0052 | 2.2875 | 0.0079 |
| <i>D. rotundatus</i> | -0.5257 | 1.1147 | 0.0879 | 2.4292 | 10.9220 |
| <i>L. cylindracea</i> | -1.3697 | -0.1054 | 0.0126 | 2.3638 | 0.0139 |
| <i>N. hammonis</i> | 1.0101 | -0.9244 | 0.1497 | 15.2739 | 12.7920 |
| <i>O. alliarius</i> | -1.4451 | -2.7767 | 0.0426 | 8.8962 | 32.8448 |
| <i>O. elegans</i> | 2.6413 | 5.3712 | 0.0030 | 2.0923 | 8.6549 |
| <i>P. pygmaeum</i> | -1.6918 | -0.3795 | 0.0158 | 4.5245 | 0.2275 |
| <i>P. subvirescens</i> | 1.4076 | 0.3170 | 0.0114 | 2.2587 | 0.1145 |
| <i>V. contracta</i> | -1.1475 | 0.7172 | 0.0496 | 6.5311 | 2.5513 |
| <i>Z. excavatus</i> | 0.9669 | -0.3249 | 0.0551 | 5.1512 | 0.5816 |

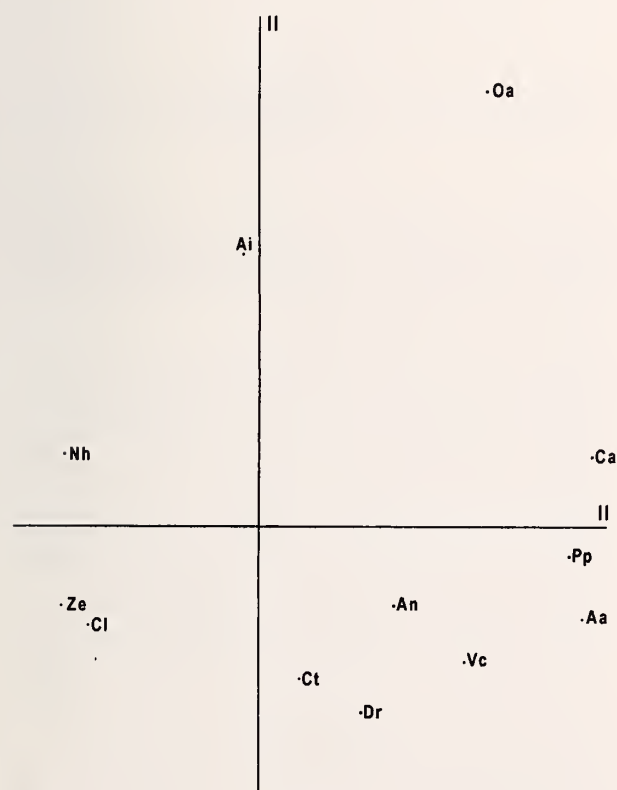


Figure 3

Ordination of the 12 species that were not downweighted on the first two axes extracted by Detrended Correspondence Analysis.

of the meadows are located on the left side. In view of this plot, the woodland gastropod community can be considered to comprise *C. aspera*, *A. aculeata*, *P. pygmaeum*, and *O. alliarius*, accompanied by *V. contracta*, *A. nitidula*, and *D. rotundatus*, while the community of open areas, meadows, comprises *N. hammonis*, *C. lubrica*, and *Z. excavatus*.

To confirm these conclusions, we calculated the centroids. To find out the centroids, a matrix was built in which the variable biotope was converted into a nominal variable. So we assigned to each sample the value 1 or 0, according to their presence or absence into the considered variable. As expected, the woodland centroid lies to the right of the plot, whereas the open-site centroids are plotted to the left (Figure 5). The riverbank centroid lies close to the origin, which is attributable to the fact that such sites represent various biotopes with highly variable characteristics intermediate between woodland and meadow. This heterogeneity of the riverbank sites makes it difficult to discriminate a clearly defined species com-

Table 4

Eigenvalues, percentage inertias, significance levels and degrees of freedom for the first four axes extracted by DCA of the 12 species.

| Axis | Eigenvalue | % Inertia | χ^2 | df |
|------|------------|-----------|----------|-----|
| I | 0.388 | 17.7 | < 0.01 | 440 |
| II | 0.287 | 13.1 | > 0.05 | 438 |
| III | 0.220 | 10.6 | > 0.05 | 436 |
| IV | 0.167 | 7.6 | > 0.05 | 434 |

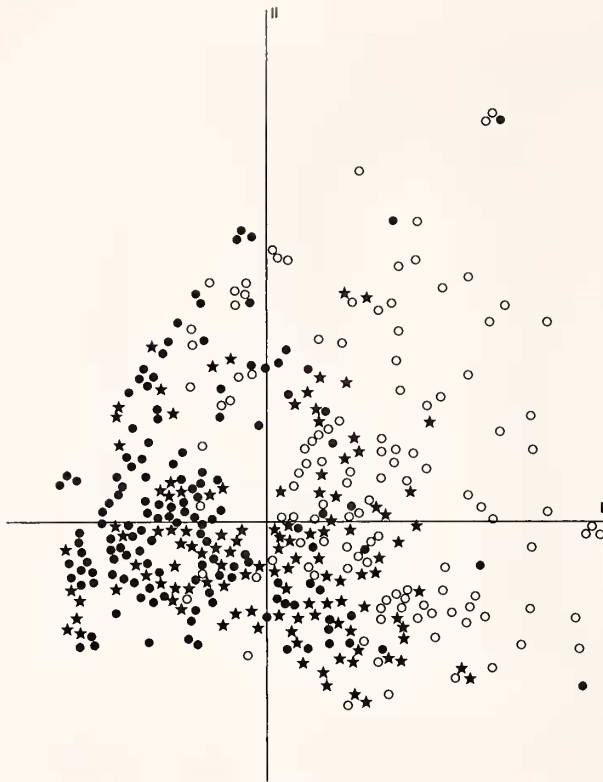


Figure 4

Plot of samples (●, meadow; ★, riverbank; ○, woodland) on the first two axes extracted by DCA of the 12 species.

munity. The characteristic that these riverbank samples have in common is constant moisture supply, which would discriminate aquatic species (not considered in the present study).

Classification

The species-abundance cut-offs selected for definition of pseudospecies for TWINSpan were 0, 3, 6, 10, 20, 40, and 100, giving up to seven pseudospecies per species. The results of the subsequent classification of sites by pseudospecies are summarized in Figure 6. The first split separated a group (group A) containing most (73%) of the woodland sites, about half (48%) of the riverbank sites, and some (26%) of the meadow sites, from a group (group B) containing most (74%) of the meadow sites, the other half (52%) of the riverbank sites, and some (27%) of the woodland sites.

The results of the classification of species by sites are summarized in Figure 7. The two species groups defined by the first split are very similar to those obtained by DCA: a first group (group A) including *A. aculeata*, *C. aspera*, *O. alliarius*, *P. pygmaeum*, *A. nitidula*, *C. tridentatum*, *V. contracta*, *Euconulus fulvus*, and *Clausilia bi-*

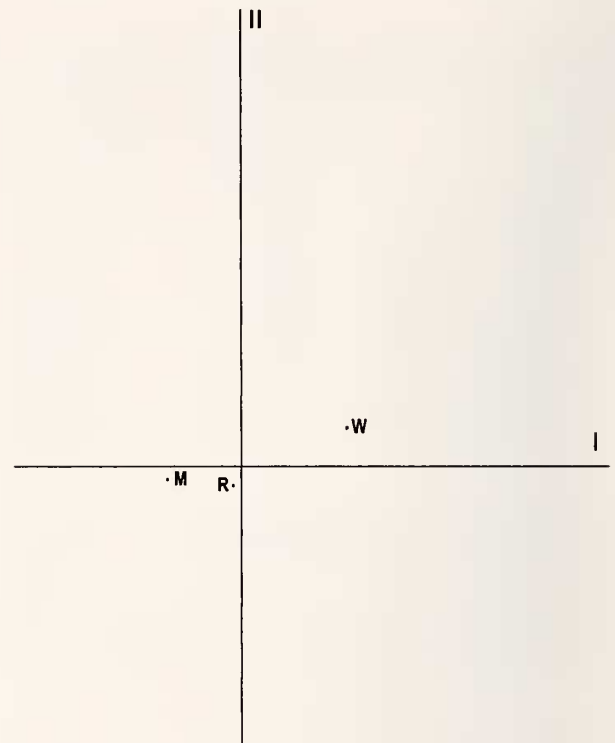


Figure 5

Centroids of the three biotopes (M—meadow; R—riverbank; W—woodland) on the first two axes extracted by DCA of the 12 species.

dentata, and a second group (group B) including *C. lubrica*, *N. hammonis*, *Z. excavatus*, *Deroceras reticulatum*, *Ponentina subvirescens*, *Deroceras lombricoides*, *Deroceras laeve*, and *Vertigo pygmaeae*.

The results of classification of sites considering the 12 species used in DCA are summarized in Figure 8. Considering the groups resulting from the first split, the indicator pseudospecies for group A (with abundance class in brackets) are *N. hammonis* (1) and *C. lubrica* (1), while those for group B are *V. contracta* (1), *A. nitidula* (1), and *A. aculeata* (1). Group A contains 79% of woodland sites, 57% of riverbank sites, and 34% of meadow sites, whereas group B contains most meadow sites, somewhat less than half of the riverbank sites, and a small proportion of woodland sites. The first split within group B separates group BB, with indicator pseudospecies *C. lubrica* (2), *C. tridentatum* (1), and *Z. excavatus* (2), containing most of the meadow sites and only a single woodland site, from group BA, containing all other group-B woodland sites. The first split within group A separates group AA, with indicator pseudospecies *C. tridentatum* (1), *A. nitidula* (1), *D. rotundatus* (1), *V. contracta* (1), *C. lubrica* (1), and *A. aculeata* (1), from group AB, with indicator species *O. alliarius* (1).

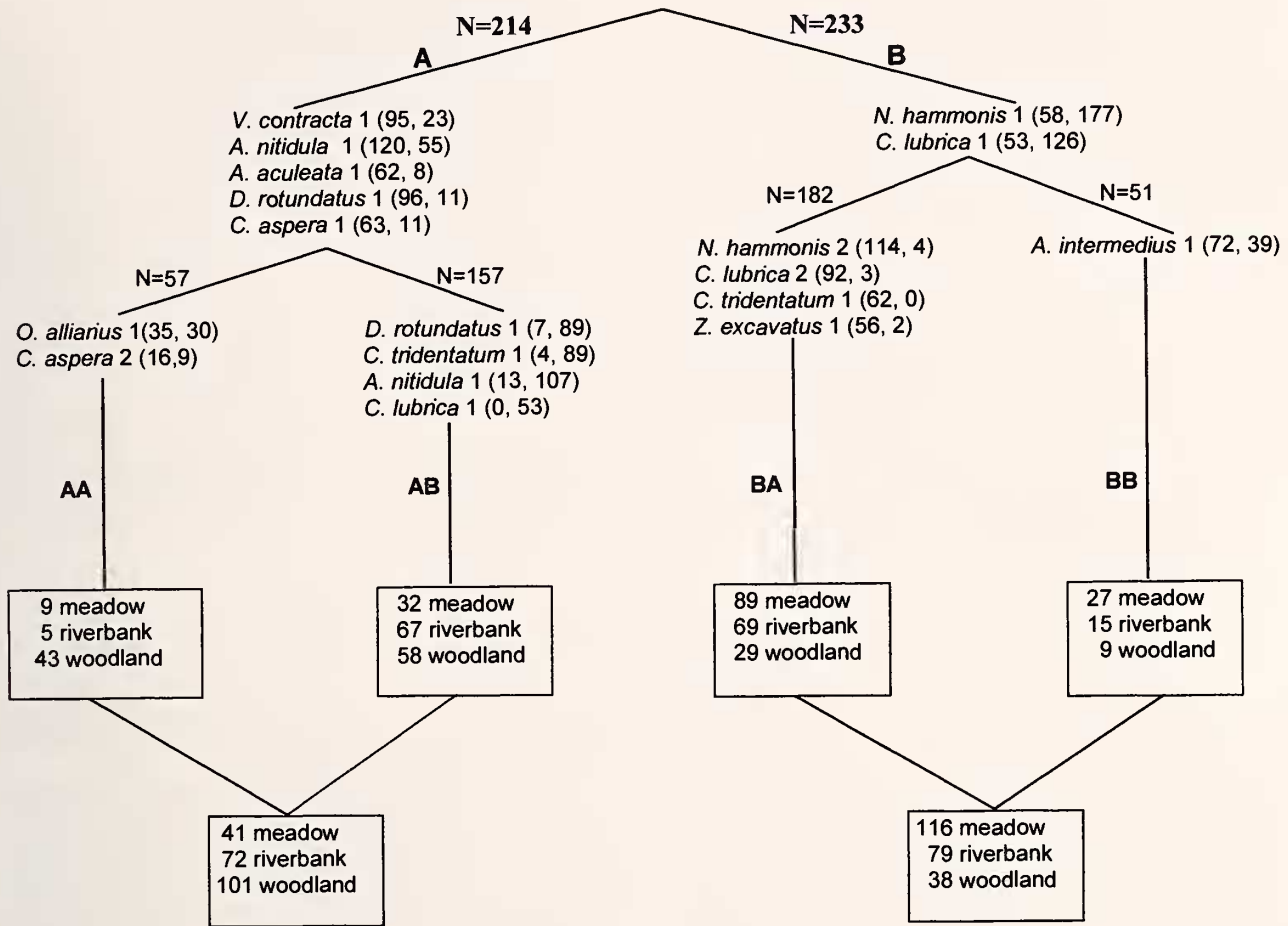


Figure 6

TWINSPLAN classification of the samples considering the 47 species, showing the indicator pseudospecies for each split.

The classification of these 12 species by sites (Figure 9) is again very similar to that obtained by DCA. The first split separates a group (group B) comprising *N. hammonis*, *C. lubrica*, and *Z. excavatus* from the rest (group A). The first species to split from group A are *C. tridentatum* and *A. intermedius*, in accordance with the more variable behavior of these taxa (as was indicated by DCA). The remaining species split into two groups: one comprising *V. contracta*, *D. rotundatus*, and *A. nitidula*, the other *P. pygmaeum*, *O. allianus*, *C. aspera*, and *A. aculeata*.

DISCUSSION

Gastropod populations exist in complex environments reflecting the interaction of numerous factors, including characteristics of the soil-humus-litter-vegetation system. This system is clearly dependent on the herb and woody layers, which contribute to litter formation, filter light,

and buffer variation in moisture levels and temperature. The resulting habitat characteristics are critical for the establishment of certain species, and variations in these factors are the cause of the observed differences among communities.

Taken together, the results of the different analyses indicate that the *C. lubrica*, *N. hammonis*, and *Z. excavatus* characterize the snail communities present in open sites (meadow). The other group comprises *C. aspera*, *O. allianus*, *A. aculeata*, and *P. pygmaeum*, with preference for wooded areas with more vegetation cover.

V. contracta, *D. rotundatus*, and *A. nitidula* form a group of companion species to the woodland gastropod community, but are also important in riverbank communities, where they are in fact more abundant.

A. intermedius and *C. tridentatum* show more irregular behavior, their presence being more homogeneously distributed, though both appear to have a stronger preference for open areas than for woodland sites.

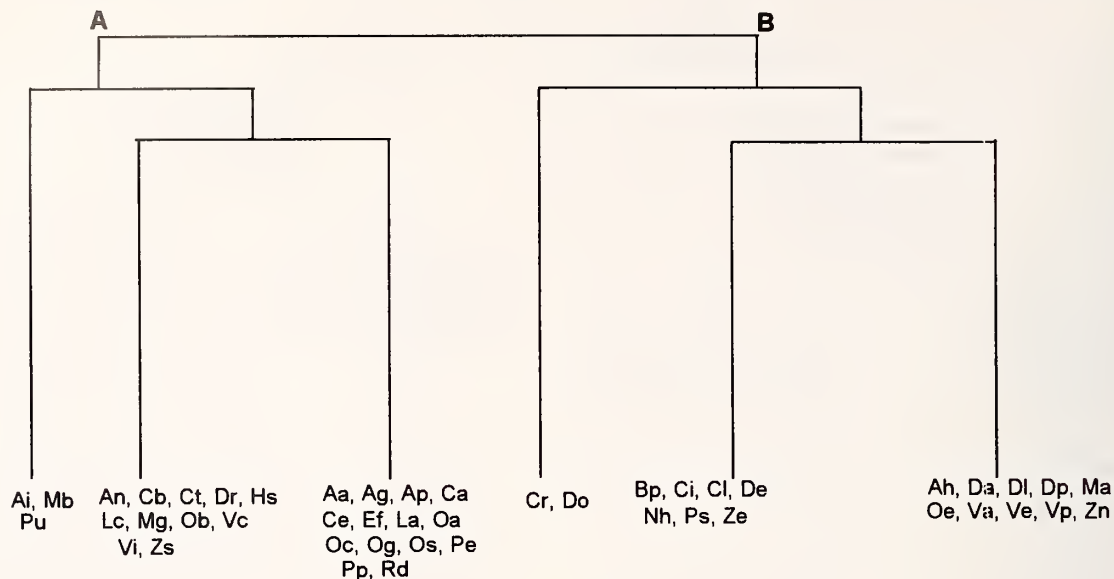


Figure 7

TWINSpan classification of the 47 species.

Although these are the only species for which statistically significant conclusions may be drawn, in view of their abundances and contribution to the ordination, valid conclusions may also be inferred for a number of other species. Notably, some species that are relatively infrequent in the sample as a whole may in fact be important components of particular habitat types that form subcategories of the major categories (woodland, riverbank, meadow). Species of this type may include the agriolimacids *D. reticulatum*, *D. lombricoides*, and *D. laeve* (which appear to show a preference for open areas), and the group comprising *P. subvirescens*, *Cochlicella barbara*, and *V. pygmaea* (particularly the latter), which is

more abundant in meadow. *E. fulvus*, by contrast, shows a preference for woodland sites.

Some authors, including Boycott (1934), whose study provided the starting point for the majority of more recent studies, have concluded that gastropods show no specific association with vegetation, and that apparent relationships between gastropods and vegetation are due more to environmental conditions than to the fact that the plants in question are food sources (since the variety of the gastropod diet means that this would be a limiting factor only under extreme conditions). Bishop (1977) considered that vegetation has no important effect on the composition of the malacofauna, but that the litter layer (which provides

Table 5

Coordinates, weights, and absolute contributions to the first two axes extracted by DCA for all 12 species included in the analysis.

| Species | Coord. axis I | Coord. axis II | Weight | Contrib. axis I (%) | Contrib. axis II (%) |
|-----------------------|---------------|----------------|--------|---------------------|----------------------|
| <i>A. aculeata</i> | 1.8491 | -0.5263 | 0.0304 | 10.39 | 0.84 |
| <i>A. intermedius</i> | -0.1065 | 1.6338 | 0.1269 | 0.14 | 33.87 |
| <i>A. nitidula</i> | 0.7637 | -0.4383 | 0.1022 | 5.96 | 1.96 |
| <i>C. aspera</i> | 1.9244 | 0.4041 | 0.0315 | 11.66 | 0.51 |
| <i>C. lubrica</i> | -1.0413 | -0.5492 | 0.1411 | 15.29 | 4.25 |
| <i>C. tridentatum</i> | 0.1860 | -0.8620 | 0.1163 | 0.40 | 8.64 |
| <i>D. rotundatus</i> | 0.5363 | -1.0580 | 0.0989 | 2.84 | 11.07 |
| <i>N. hammonis</i> | -1.1624 | 0.4360 | 0.1683 | 22.74 | 3.20 |
| <i>O. alliaris</i> | 1.3454 | 2.5484 | 0.0479 | 8.67 | 31.10 |
| <i>P. pygmaeum</i> | 1.7727 | -0.1755 | 0.0177 | 5.56 | 0.05 |
| <i>V. contracta</i> | 1.1568 | -0.7654 | 0.0558 | 7.46 | 3.26 |
| <i>Z. excavatus</i> | -1.1854 | -0.4309 | 0.0620 | 8.71 | 1.15 |

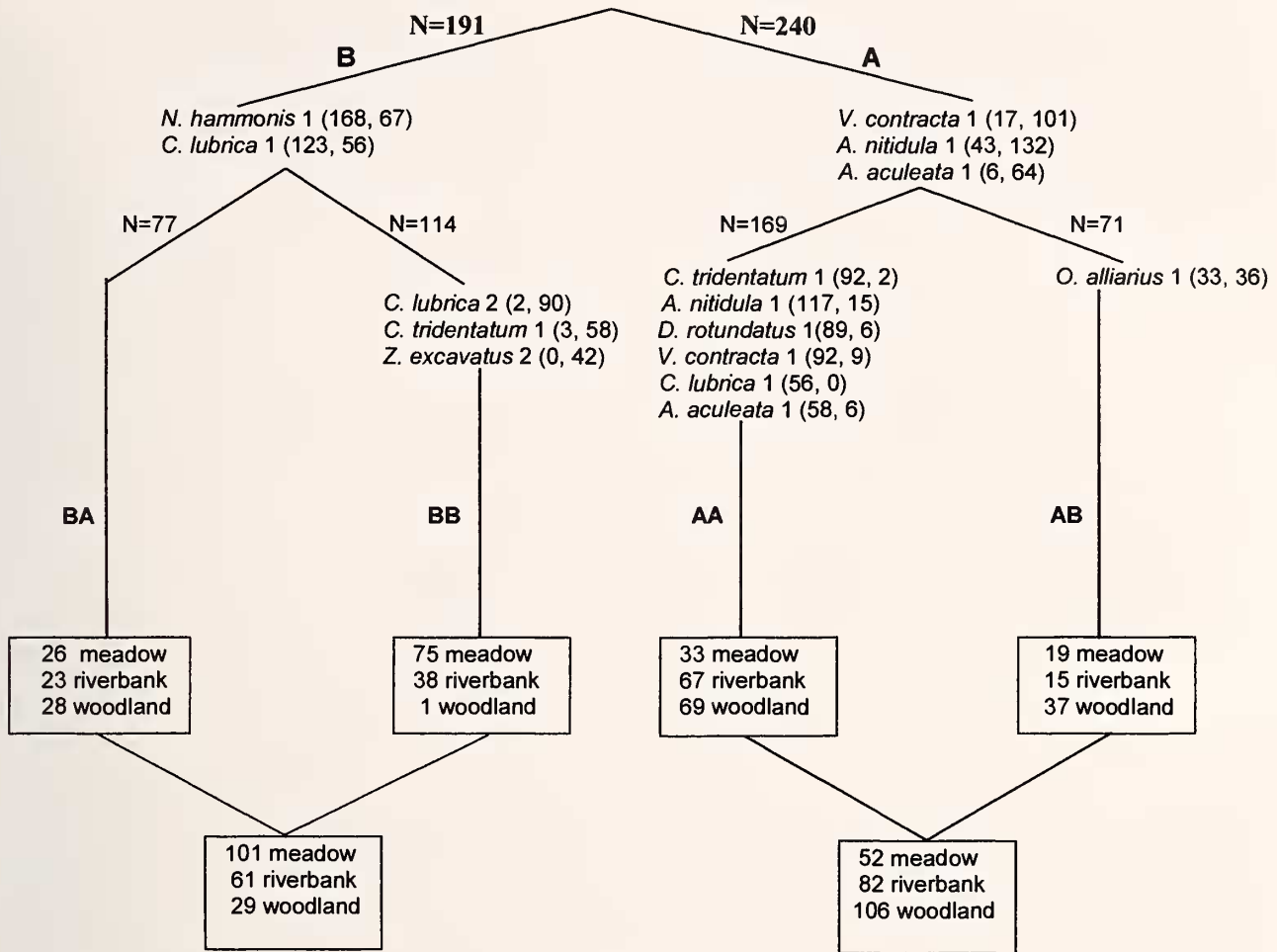


Figure 8

TWINSpan classification of the samples, considering the 12 species considered in the second DCA.

food and shelter) has a marked effect, important factors being mineral content, surface bacterial and fungal populations, and the amount of usable litter. Locasciulli & Boag (1987) pointed out that litter layer characteristics depend on the overlying vegetation, and took as their starting point the assumption that gastropods do not use the litter layer directly, but rather nutrients derived from it; nevertheless, they stressed the importance of the litter layer for providing a stable microclimate.

In the present study, we have taken as our starting point the view that even the most common and most euryecious species do not occur in all vegetation types; all species prefer some biotopes over others, so that different biotopes can be considered rich or poor depending on the conditions that they offer to the specific demands of the species in question. Thus each biotope may contain characteristic associations, and it is thus probably the condi-

tions created by that biotope that determine the establishment of the malacofauna.

Woodland vegetation may itself provide the gastropod fauna with the necessary conditions for survival: it buffers variations in temperature and humidity, and provides shelter and varied microhabitats such as tree roots, fallen trunks, hollows, together with a usable humus and litter layer. The tree cover performs a basic microclimatic role, which is probably more important than the composition of the litter layer. It is indeed the presence or absence of climate-buffering tree cover that largely explains the difference in malacofauna between woodland and meadow biotopes: the latter are exposed to marked daily and seasonal variations in temperature, humidity, and light intensity (Dillon, 1980; Boag & Wishart, 1982; Curry, 1994). Species that occur preferentially in meadow are probably more resistant to such variation, and escape its effects by

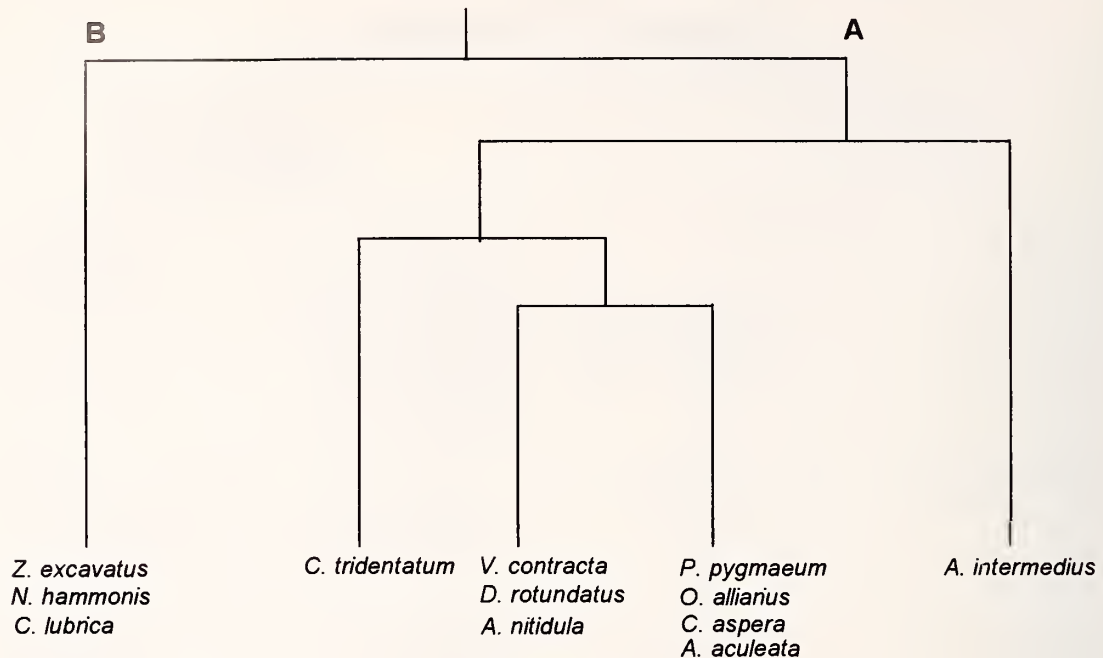


Figure 9

TWINSpan classification of the 12 species considered in the second DCA.

burrowing into the soil (Stephenson, 1966 in Peake, 1978; Outeiro et al., 1989; Outeiro et al., 1993), or are more influenced by other non-microclimatic factors first, such as biotope factors, or soil factors, or factors not considered in the present study, such as the quality of the litter or the herb layer.

Riverbanks constitute such a heterogeneous category that fauna of both types are present, especially species at the limits of the requirements of the other biotopes. These habitats thus probably behave as ecotones, as well as being favorable because of water availability.

In order to facilitate comparison of our results with those of previous studies, we have summarized previous results in Table 6. Like us, most authors have reported *C. lubrica* and *N. hammonis* to be species of meadow, though only Riballo (1990) also included *Z. excavatus* as the third characteristic species of this community. Previous reports of species characteristic of woodland communities, however, show some discrepancies. For example, Alonso (1977) concluded that *C. lubrica* is characteristic of poplar groves. This is probably attributable to the particular characteristics of poplar groves, in which trees are planted in existing meadow, where *C. lubrica* was probably already present.

Bába (1981) likewise considered *C. lubrica* to be a constant species within the malacofauna of woodland sites. This author's aim was to identify relationships between the successional series of gastropod communities and plant communities along a river. The only habitats

considered were woodland biotopes, characterized by various moisture and temperature indices; there was thus no comparison with other biotopes. Similar conclusions were reached by Wäreborn (1982), who considered *N. hammonis* and *C. lubrica* to be characteristic of woodland (again the only biotope considered), though it should be stressed that the characterization of biotopes in terms of malacofauna was not one of the goals of this study, so that there was no comparison with other biotopes. This author also found that *C. lubrica* may occur at high abundance in meadow. Waldén (1955) reported that *C. lubrica* is a species typical of woodlands, but this conclusion was not based on a uniform sampling strategy (16 samples were obtained from woodland sites, versus only four from open sites). This author likewise reported that *C. lubrica* may be abundant in swamps and marshes. Note, however, that Waldén's data analysis (using percentage abundances) is not directly comparable with that used in the present study.

The few previous studies to consider *Z. excavatus* have concluded that it is a woodland species (Boycott, 1934; Bishop, 1977; Anderson, 1983); this contrasts with the present study, and with Riballo (1990), who found that *Z. excavatus* appears to be characteristic of meadow. Riballo (1990) states that the distribution of *Z. excavatus* is wider than has been suggested by some previous authors; indeed, Anderson (1983) also found this species in meadow, and remarked that in acid soils (as in the present study) it typically occurs in association with *N. hammon-*

Table 6

Summarized findings of previous studies for the 12 species considered showing whether each species is judged to be characteristic of meadow (♣), characteristic of woodland (●), or ubiquitous (◆).

| Authors | Cl | Nh | Zc | Ca | Oa | Aa | Pp | Vc | An | Dr | Ct | Ai |
|-------------------------|----|----|----|----|----|----|----|----|----|----|----|----|
| Alonso, 1977 | ● | | | | | | ● | | | | ● | |
| Anderson, 1983 | | | ● | ● | ● | ● | | | | | | |
| André, 1982 | ♣ | | | | | ● | ● | ● | | ● | | |
| Bába, 1981 | ● | ● | | | | | ● | ● | | | | |
| Badie & Rondelaud, 1979 | ♣ | ♣ | | | | | | | | | | |
| Bishop, 1977 | | ● | ● | ● | ● | ● | ● | | ● | ● | | ● |
| Boycott, 1934 | | | ● | | ● | ● | ● | | ● | ● | | |
| Cameron, 1973, 1978 | | | | | ● | ● | ● | ● | ● | ● | | ◆ |
| Cameron et al. 1980 | | | | | ● | ● | ● | | | ● | | |
| Frank, 1979 | ♣ | ♣ | | | | ● | ● | | | ● | ● | |
| Hermida et al., 1994 | ♣ | ♣ | | | | ● | ● | ● | ● | | | ◆ |
| Jourdin et al., 1985 | ♣ | | | | | | | | | | | |
| Kornig, 1989 | ♣ | ♣ | | | | | | | | | | |
| Mason, 1974 | | | | | ● | ● | ● | ● | ● | ● | ● | |
| Matzke, 1976 | ♣ | | | | | | | | | | | |
| Meier, 1987 | ♣ | ♣ | | | | | | | | | | |
| Mordan, 1977 | | ♣ | | | | | | | | | | |
| Ojea & Anadón, 1983 | ♣ | | | | | | | ● | | | | |
| Ojea et al., 1987 | ♣ | ♣ | | | | ● | ● | ● | ◆ | ● | ◆ | ◆ |
| Outeiro, 1988 | ♣ | ♣ | | | ● | ● | ● | ● | | ● | ◆ | ◆ |
| Outeiro et al., 1989 | | | | | | | ● | | | | | |
| Paul, 1975a,b | | | | ● | | ● | | | ● | ● | ● | |
| Paul, 1978a,b | ◆ | | | | | ● | ● | | ● | ● | ● | |
| Phillipson & Abel, 1983 | | | | | | ● | ● | ● | ● | ● | ● | |
| Radea & Mylonas, 1992 | | | | | | ● | ● | | | | | |
| Riballo, 1990 | ♣ | ♣ | ♣ | ● | | ● | ● | ● | ● | ● | | ◆ |
| Riballo et al., 1995 | | | | | | ● | ● | ● | ● | ● | ● | |
| Solhøy, 1981 | ♣ | ♣ | | | | | ● | | ● | | | ◆ |
| South, 1992 | | | | | | | | | | | | ◆ |
| Štamol, 1993 | | | | | ● | ● | ● | | | | | |
| Tattersfield, 1990 | | | | | | | | | | | | ◆ |
| Valovirta, 1967, 1979 | | | | ● | ● | ● | ● | | ● | | | |
| Waldén, 1955 | ● | | | | | ● | ● | ● | | | ● | |
| Wäreborn, 1982 | ● | ● | | | | ● | | | ● | ● | ● | |

is. Boycott (1934) did not find this species in his woodland sites and, although he referred to it as a woodland taxon, he stated that its special characteristics (notably calciphobia and sensitivity to competition) lead it to live "where it can" and not "where it would like to." In any case, there have been few ecological studies of this species, and there is a shortage of data to facilitate statistical investigation of putative relationships with particular types of biotope.

Our results for both *P. pygmaeum* and *A. aculeata* agree closely with previous reports; both have consistently been identified as woodland species. Similarly, our results for *C. aspera* and *O. alliarius*, classified in the present study as characteristic of woodland, likewise show close agreement with previous studies. The species classified in the present study as woodland-community companion species have often been described as woodland species, supporting our findings.

The present results indicate that *C. tridentatum* and *A. intermedius* should be considered as ubiquitous species, whereas some previous studies have classified these species as characteristic of woodland. This difference is probably attributable to the fact that these previous studies considered only woodland sites, therefore the presence in this biotope of ubiquitous species seems logical. Moreover, some of the species classified in the present study as characteristic of meadow or riverbank have previously been classified as ubiquitous by previous authors.

It should be borne in mind that there have been few studies in which the sampling method or the statistical treatment of the data have been directly comparable with those used in the present study. Furthermore, most previous studies included consideration of species that are absent from our region, or that did not show significant habitat preferences in the present study. André (1982) studied terrestrial mollusk populations in *Quercus pubes-*

cens communities, and by means of multivariate analysis techniques obtained an ordination of samples and species that is very similar to that obtained in the present study. He likewise characterized two contrasting groups of samples, on the one hand samples from open sites, and on the other, samples from sites with taller vegetation cover. Many of the species present in this author's samples were not present in our samples. Nevertheless, our results for those species present in both studies show close agreement, with *C. lubrica* characteristic of open sites, and *D. rotundatus*, *E. fulvus*, *A. aculeata*, and *P. pygmaeum* characteristic of woodland or semi-woodland sites.

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APPENDIX I

List of species detected in the present study, in each case showing species code (e.g., **Aa**), species name and authority, and total number of individuals detected.

- Aa:** *Acanthinula aculeata* (Müller, 1774) (191)
Ag: *Azeca goodalli* (A. Férussac, 1821) (30)
Ah: *Arion hortensis* A. Férussac, 1819 (9)
Ai: *Arion intermedius* Normand, 1852 (1220)
An: *Aegopinella nitidula* (Draparnaud, 1805) (1024)
Ap: *Aegopinella pura* (Alder, 1830) (4)
Bp: *Balea perversa* (Linnaeus, 1758) (5)
Ca: *Columella aspera* Waldén, 1966 (175)
Cb: *Clausilia bidentata* (Ström, 1765) (121)
Ce: *Columella edentula* (Draparnaud, 1805) (3)
Ci: *Candidula intersepta* (Poiret, 1801) (15)
Cl: *Cionella lubrica* (Müller, 1774) (3167)
Cr: *Cochlicella barbara* (Linnaeus, 1758) (395)
Ct: *Carychium tridentatum* (Risso, 1826) (2713)
Da: *Deroceras agreste* (Linnaeus, 1758) (2)
De: *Deroceras reticulatum* (Müller, 1774) (108)
Dl: *Deroceras laeve* (Müller, 1774) (42)
Do: *Deroceras lombricoides* (Morelet, 1845) (63)
Dp: *Deroceras panormitanum* (Lesson & Pollonera, 1882) (1)
Dr: *Discus rotundatus* (Müller, 1774) (1723)
Ef: *Euconulus fulvus* (Müller, 1774) (84)
Hs: *Helicodiscus* sp. Morse, 1864 (81)
La: *Leiostylia anglica* (Wood, 1828) (49)
Lc: *Lauria cylindracea* (Da Costa, 1778) (560)
Ma: *Milax gagates* (Draparnaud, 1801) (8)
Mb: *Mengoana brigantina* (Da Silva, 1867) (2)
Mg: *Ashfordia granulata* (Alder, 1830) (43)
Nh: *Nesovitrea hammonis* (Ström, 1765) (3223)
Oa: *Oxychilus alliaris* (Miller, 1822) (371)
Ob: *Oestophora barbula* (Rossmässler, 1838) (81)
Oc: *Oxychilus cellarius* (Müller, 1774) (29)
Oe: *Oxyloma elegans* (Risso, 1826) (80)
Og: *Oxychilus glaber* (Rossmässler, 1835) (15)
Os: *Oestophora silvae* Ortiz de Zárate, 1962 (32)
Pe: *Pomatias elegans* (Müller, 1774) (1)
Ps: *Ponentina subvirescens* (Bellamy, 1839) (208)
Pp: *Punctum pygmaeum* (Draparnaud, 1801) (95)
Rd: *Rumina decollata* (Linnaeus, 1758) (20)
Pu: *Paralaoma caputspinulae* (Reeve, 1852) (33)
Va: *Vertigo antivertigo* (Draparnaud, 1801) (3)
Vc: *Vitrea contracta* (Westerlund, 1871) (391)
Ve: *Vallonia excentrica* Sterki, 1892 (364)
Vi: *Vitrina pellucida* (Müller, 1774) (9)
Vp: *Vertigo pygmaea* (Draparnaud, 1801) (77)
Ze: *Zonitoides excavatus* (Alder, 1830) (1024)
Zn: *Zonitoides nitidus* (Müller, 1774) (1)
Zs: *Zenobiella subrufescens* (Miller, 1822) (17)
 Total 17,902